

A shallow-living benthic Rhodaliid siphonophore: citizen science discovery from Papua New Guinea

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Abstract

Benthic siphonophores of the family Rhodaliidae (Cnidaria, Hydrozoa) are extremely fragile, difficult to collect, and therefore little studied. Only a few records exist worldwide, so their ecology remains largely unknown. Rhodaliids have been found at most depth horizons, but until now were believed to mainly inhabit deeper water over continental shelves, with only a few records from ca. 100 m. In this paper, a new rhodaliid is described based on an underwater photograph provided by a recreational diver *via* Facebook. This observation was made in Milne Bay (Papua New Guinea) at a depth of 26–27 m, and constitutes the shallowest record so far for any rhodaliid. The specimen was tentatively identified as *Archangelopsis typica* based on observable morphological characters and an approximate estimate of connectivity between all rhodaliid species in the Indo-Pacific region. Additionally, we highlight the scientific potential of citizen science.

Introduction

Rhodaliids are an unusual family of physonect siphonophores (Cnidaria: Hydrozoa), with a relatively large pneumatophore, or gas-filled float, which suspends the animal just above the bottom; it attaches to the bottom *via* a number of much extended gastrozooid tentacles. Rhodaliids inhabit all oceans, with the only exceptions so far being the Mediterranean and Arctic, live at all depths from 100 m down to 3670 m, and exhibit species-specific depth ranges (Mapstone *et al.* 2016, Table I). They are delicate animals of small size, only occasionally encountered worldwide, and even less frequently collected and studied in the laboratory due to their fragility. Thus, they have never been reared in captivity, and their life cycles and larval stages remain largely unknown.

Public participation in scientific research, referred to as citizen science, has become popular recently, with growing interest in worldwide projects like “*JellyWatch*” (www.jellywatch.org), that gather data otherwise unavailable to regular scientific projects (Silvertown 2009). Citizen science is based on the assumption that almost everyone can contribute to scientific research without having extensive knowledge on a given subject. Such contributions are especially important in marine environments, where the distribution, patchiness and general fragility of life forms can impose severe constraints on research. Recreational scuba diving is an increasingly popular sport, and divers often carry high quality underwater camera equipment, which can potentially provide new scientific data of significant spatial resolution. Near one popular dive location, the wreck of the ‘Muscoota’ in Milne Bay, Papua New Guinea (PNG), a diver, Andrey Ryanskiy encountered the present rhodaliid, on a sand and mud flat bottom at 26–27 m on the southern side of Milne Bay six miles south of Alotau (10°24' E 150°24' E). He placed his image on “*ID Please (Marine Creature Identification)*”, an open Facebook group constituting a discussion platform for recreational divers/snorkelers worldwide who can ask taxonomists for identification of animals captured in their photographs (<https://www.facebook.com/groups/idpls/?fref=ts>).

In this study, we evaluate the morphological and ecological attributes of the photographed rhodaliid, and suggest a tentative identification based on observable characters and comparison with other rhodaliids, in particular species previously described and studied from the Western Pacific and Indian Oceans.

Results

Important characters for rhodaliid identification include the texture and colour of the pneumatophore and the adjacent aurophore or gas gland, the type of corm and cormidia present, and the number of whorls and zooid types on the corm (Mapstone *et al.* 2016, Table II). Pneumatophores and aurophores can be smooth or papillate, corms may be hollow or solid and thin or thick-walled, cormidia may be borne separately on individual stems (monogastric) or in groups of up to three on a single stem or stalk (polygastric). A single cormidium can bear one or two types of gastrozooid, a gonodendron with gonopalpons (in all but one species) and, when mature, male or female gonophores. These characters have been summarized for all genera by Mapstone *et al.* (2016, Table II). Colour and patterning can also be diagnostic, with most rhodaliids displaying an overall bright or pale orange colouration (*Dromalia*, *Stephalia*, *Thermopalia*, *Tridensa* and Mid-Atlantic Species A in Mapstone *et al.* 2016), or having a pale and almost white overall colour with bright pigments only on the pneumatophore and/or certain cormidial zooids. Examples of the latter include *Arancialia* (Hissmann 2005), *Archangelopsis* (Hissmann *et al.* 1995; Hissmann 2005), *Rhodalia* (Araujo 2012), and Mid-Atlantic Ridge Species B in Mapstone *et al.* (2016).

The present PNG rhodaliid is pale overall, with bright pigments on the pneumatophore, the discernible gastrozooids (a prominent red stripe along the length of each), and the interior portions of the cnidobands of the tentilla (stinging batteries) on the tentacles (Fig. 1). In addition, the ratio of discernible gastrozooids to extended tentacles is approximately 1:1, suggesting that the animal in the PNG specimen photograph is probably monogastric.

Other characters discernible in the PNG specimen photograph are labelled in the interpretive drawing (Fig. 1). They include a distinctive yellow apex and single bright yellow circumferential ring on the pneumatophore, completely transparent nectophores in a corona around the pneumatophore, gastrozooids each with a small yellow distal tip (the proboscis) and longer proximal stomach region with prominent single red stripe, gonopalpons each with a white tip (also termed a proboscis), one or two dense opaque spots just proximal of the tip, and some weak red stripes on the stomach region. Such gonopalpons are borne on a gonodendron in rhodaliids, but no gonophores are identifiable by the authors in the PNG image. The tentilla on some of the attached tentacles are extended for feeding, with a short pedicel, loosely coiled white and pink cnidoband and elongate single distal terminal filament (Fig. 1). Altogether these colony characters suggest that the PNG specimen should be assigned to the genus *Archangelopsis*, and, most probably, to the species *A. typica*.

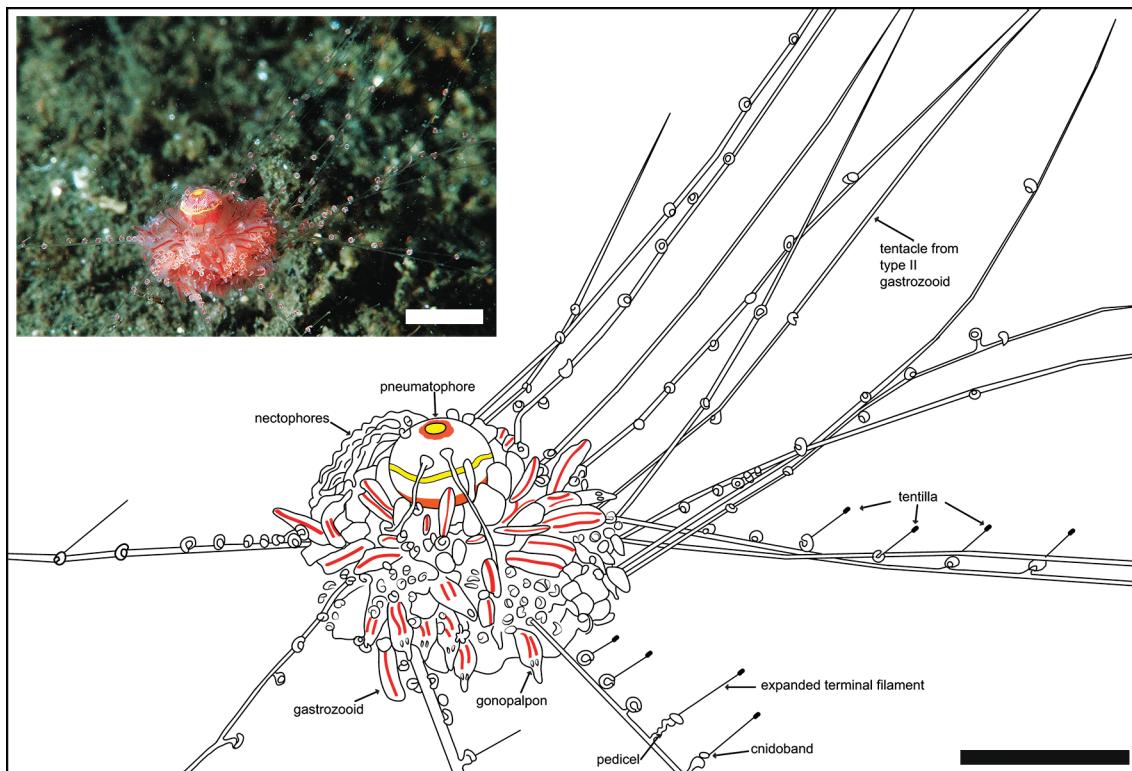


FIGURE 1. Enhanced photograph of the Papua New Guinea rhodaliid (insert) and a vector drawing of the specimen. Scale bars 10 mm. Original version of the photograph (by Andrey Ryanskiy) is accessible under <https://dx.doi.org/10.6084/m9.figshare.5411035>.

Discussion

Identification. Monogastric cormidia have so far been identified in only two genera of rhodaliids: *Arancialia* and *Archangelopsis* (see Mapstone *et al.* 2016, Table II). *Arancialia* is monotypic for *A. captonia* from off South Africa (Hissmann 2005), while *Archangelopsis* comprises two species, *A. typica* and *A. jagoa*. The latter genus was introduced by Lens & van Riemsdijk (1908) for three specimens of *A. typica* collected during the Dutch Siboga Expedition to Indonesia 1899–1900. A fourth specimen was found in the East China Sea off SW Japan during the 1906 Albatross Expedition (Bigelow 1913). Almost a century later a second species *A. jagoa* was introduced for specimens from the Gulf of Aqaba in the Red Sea and the Comores Islands in the western Indian Ocean (Hissmann *et al.* 1995; Hissmann 2005).

Arancialia has a smooth pneumatophore like that of *Archangelopsis* species, but differs from the PNG rhodaliid in being translucent with only a faint band of red lines and white dots around the circumference (Hissmann 2005). In addition, *A. captonia* has only been collected off South Africa (see Mapstone *et al.* 2016, Fig. 1).

The pneumatophore of the PNG rhodaliid is somewhat similar to that of *Archangelopsis jagoa* in life, but differs from it in having a narrow yellow-coloured band around the maximum circumference (Fig. 1). In *A. jagoa* there are up to 6 circular pigment rings around the pneumatophore, including a particularly broad and distinctive white band just above the maximum circumference (Hissmann *et al.* 1995, Fig. 2a, d; Hissmann 2005, Fig. 1d, g). The PNG pneumatophore is also two to three times larger than the maximum diameter noted for *A. jagoa* (Hissmann *et al.* 1995), and in this respect, resembles the larger pneumatophores described by Lens & van Riemsdijk (1908) and Bigelow (1913) for *A. typica*. Unfortunately, the colouration of *A. typica* was never described (Lens & van Riemsdijk 1908), thus precluding subsequent comparisons.

The aurophore is papillate in both *Archangelopsis jagoa* (Hissmann *et al.* 1995) and *A. typica* (Lens & van Riemsdijk 1908), but unfortunately is not discernible in the PNG rhodaliid, possibly because it is hidden from view on the far (ventral) side on the corm (Fig. 1).

The radial canals and ostial ring canal of the nectophores of the PNG rhodaliid are colourless in life, giving them a translucent appearance (Fig. 1). In contrast, the canals of *Archangelopsis jagoa* nectophores are orange-red in colour and show prominently in several of the published images of this species (Hissmann *et al.* 1995 Fig. 2d, Hissmann 2005 Fig. 1g). This lack of pigmentation probably also applies to the canals of the bracts of the PNG rhodaliid, as discussed further below.

The gastrozooids in the PNG rhodaliid are similar to those apparent in published figures of *Archangelopsis jagoa* by Hissmann *et al.* (1995, Fig. 2 a–d), and are disposed in one or more whorls around the corm (Fig. 1). In *A. jagoa* they were identified as type II gastrozooids, because of their position on the corm, and their elongate tentacles (Hissmann *et al.* 1995). Later, type I gastrozooids were also identified in *A. jagoa* specimens from the Comores Islands, on the corm base on very thin pedicels (Hissmann 2005). Similar type I gastrozooids occur in many other rhodaliid species (Pugh 1983; Mapstone *et al.* 2016, Table II) and all have a short tentacle or none; their function is to collect prey captured by the tentilla of the type II gastrozooid tentacles and either ingest it themselves or transfer it to type II gastrozooids for digestion (Pugh 1983; Hissmann 2005). The tentacles from type II gastrozooids are noted to be thicker in *A. jagoa* than in most other rhodaliids (Hissmann *et al.* 1995), and this also holds for the PNG rhodaliid tentacles, particularly at their proximal ends (Fig. 1), suggesting that thicker tentacles may be a character of generic rather than specific importance in rhodaliids. However, the corm base and any possible type II gastrozooids emerging from it could not be discerned in the PNG rhodaliid due to the angle at which the image was taken.

Tentilla from type II gastrozooids in the PNG specimen are also similar to those shown for *Archangelopsis jagoa* by Hissmann *et al.* (1995, Fig. 5), as well as the tentilla in published figures of *Rhodalia* and *Thermopalia* (Pugh 1983, Figs 22, 38b). This observation suggests that tentillum structure may also be of generic importance in rhodaliids, whether preserved intact or imaged *in situ*. However, tentilla of the PNG specimen clearly differ from those of *Dromalia* (Pugh 1983 Fig. 31c) and *Tridensa* (Hissmann 2005 Fig. 4), in lacking a double swelling at the distal end of the cnidoband. In the extended tentacle emerging bottom right from the PNG specimen in Fig. 1, each tentillum is shown to be of similar construction to that of *A. jagoa*, comprising a short pedicel, a cnidoband of ca. two loose coils, and a long extended distal terminal filament. However, it is bicoloured in the PNG specimen with an outer row of presumed smaller white haploneme nematocysts and an inner row of presumed larger red heteroneme nematocysts (Fig. 1). In *A. jagoa* the tentillum is orange coloured in life, and is likely to be specifically different to that of the PNG rhodaliid. The exact origin of each tentillum appears to be from the proximal end of each tentacle segment in the PNG specimen, as in *A. jagoa*, whereas in *A. typica* it apparently arises from the mid-region of each segment (Hissmann *et al.* 1995). This suggests perhaps that the PNG rhodaliid represents a third and new species of *Archangelopsis* rather than an additional specimen of *A. typica*, but such a conclusion can only be verified by the collection of fresh PNG rhodaliid material.

Gonopalpons are also identifiable in the PNG rhodaliid shown in Fig. 1, and are similar morphologically to those illustrated by Hissmann *et al.* (1995, Fig. 4) for *Archangelopsis jagoa*. In the latter species some gonopalpons expanded considerably to attach to the walls of the tank in live individuals observed in Eilat after capture (see Hissmann *et al.* 1995, Fig. 2 a–b). However, this observation was later concluded to be atypical since in further specimens collected from the Comores Islands, such behaviour was not observed. A number of retracted gonopalpons are present in the PNG rhodaliid, as shown in Fig. 1, and this similarity of gonopalpons suggests that this character could also be of generic importance in *Archangelopsis*. The proboscis of these zooids is white, with one or two optically dense white swellings at the proximal end (Fig. 1).

Rhodaliids also have bracts, with each arising from the proximal end of the cormidial stem in *A. jagoa* and expanding into a triangular facet distally (Hissmann 2005, Fig. 13). In the latter species, the bracteal canal divides at the distal end and becomes pigmented a dark red. Unfortunately, no bracts are discernible in the PNG rhodaliid, which suggests, as noted above, that bracts may be totally transparent, like the nectophores, and perhaps lack any red pigmentation in the bracteal canals.

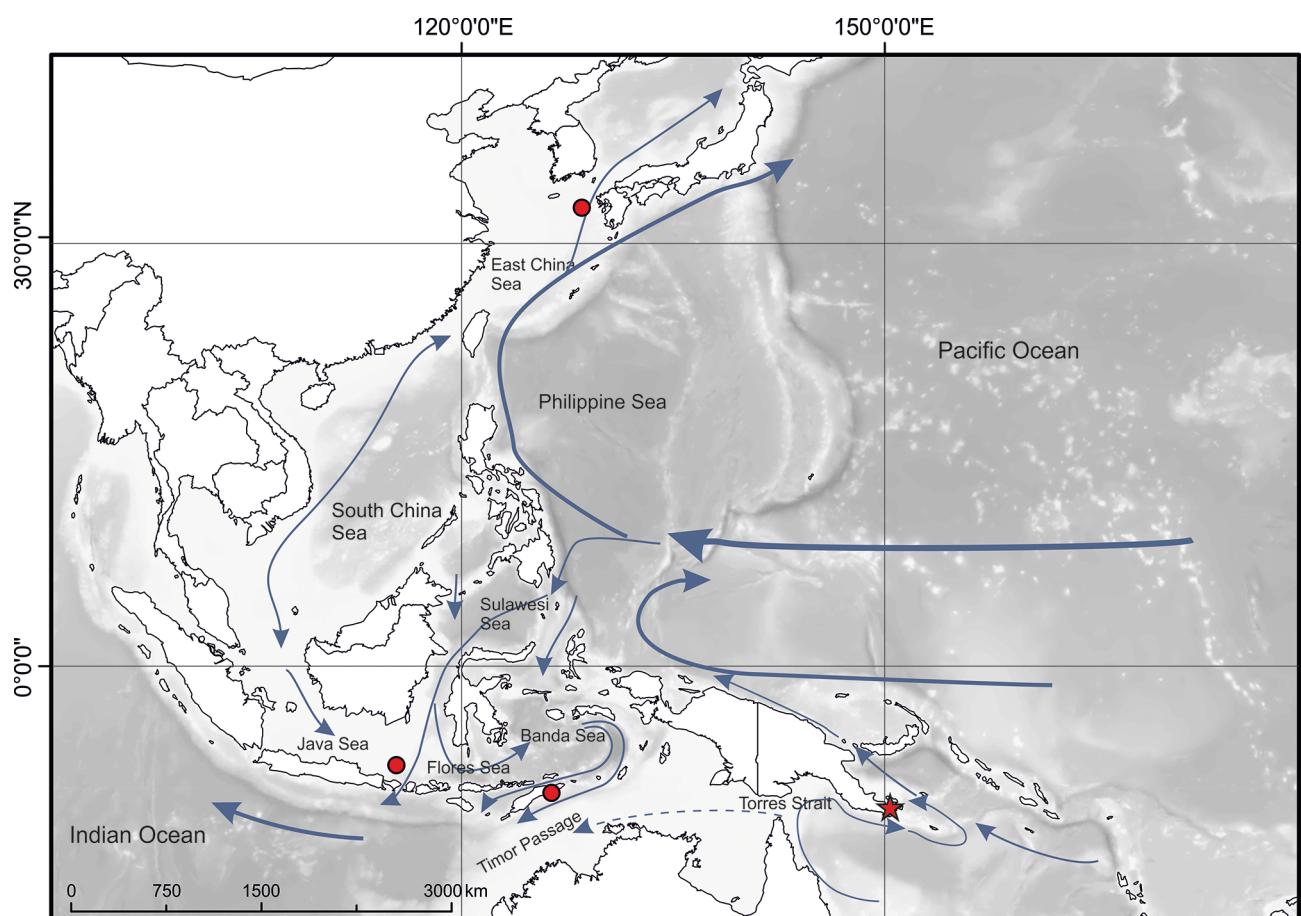


FIGURE 2. Distribution map of all extant records of *Archangelopsis typica* (circles) and of the PNG rhodaliid (star) with plotted currents systems showing main surface currents (during the southwest monsoon season). Dashed line marks extremely low water flow (Wolanski *et al.* 2013).

Connectivity of rhodaliids. Three other valid rhodaliid species have been described from the western Pacific and Indonesian region, which could perhaps have connectivity with the PNG rhodaliid. These include two species of the genus *Tridensa* from Indonesia, *T. sulawensis* and *T. rotunda* (Hissmann 2005), and *Steleophysema auophora* from Japanese waters (Pugh 1983). A fourth tentative species, *Stephalia bathyphysa* was taken off New Zealand by the Challenger Expedition in 1874, but is no longer extant (Pugh 1983). All these species differ from the PNG rhodaliid in having polygastric cormidia, though for *S. bathyphysa* this character is based solely on Haeckel's original figure (Pugh 1983). Even if *S. bathyphysa* is a valid species, connectivity with the PNG specimen is unlikely because New Zealand is isolated from PNG waters by the Pacific Equatorial Countercurrent. In *Tridensa*, the pneumatophore has irregular stripes of orange, red and white pigment (Hissmann 2005), but lacks the prominent circumferential bands typical of *Archangelopsis jagoa* and the PNG specimen. In addition, *Tridensa* has pigmented canals in the nectophores and bracts,

and large type I gastrozooids which are disposed independently around the corm (Hissmann 2005). Thus, even if connectivity exists between the *Tridensa* species from off Sulawesi and the PNG specimen, the morphological characters of *Tridensa* are dissimilar. *S. aurophora* from off Sagami Bay in the Kuroshio Current could perhaps also have connectivity with the PNG rhodaliid, but again, its morphological characters are dissimilar.

Morphological evidence suggests that the PNG specimen belongs to the genus *Archangelopsis*. Connectivity with known specimens of *A. jagoa* is unlikely, since the latter is restricted to the western region of the Indian Ocean and Gulf of Aqaba in the Red Sea (Hissmann 2005), some 115° latitude west of the record for the present specimen, from Milne Bay, PNG. Bearing in mind the rather short life span of typical siphonophore larvae (Carré 1969), it seems unlikely that larvae from the PNG rhodaliid could have travelled such a great distance to the Comores Islands in the western Indian Ocean. The distribution of the second *Archangelopsis* species, *A. typica*, is more likely to overlap with that of the PNG rhodaliid (Fig. 2).

The interplay of the relatively complex current system, the Indonesian Throughflow, and diversified seafloor topography may explain the distribution of *Archangelopsis typica* throughout the Central Indo-Pacific. Having possibly originated somewhere in the Coral Sea, *A. typica* is most likely to have reached Indonesian waters *via* the Hiri, or Coral Sea Coastal, Current, which reflects eastwards in the Gulf of Papua (Wolanski *et al.* 2013) to flow through and around the Louisiade Archipelago northwards into the Solomon Sea, continuing northwest along the northern coast of Papua New Guinea and Irian Jaya as the New Guinea Coastal Current (NGCC) (Ganachaud *et al.* 2014). From here larvae could have become entrained in currents entering the Banda Sea and the Sulawesi (Celebes) Sea as part of the Indonesian Throughflow (Gordon *et al.* 2012); these currents connect to the two sites where *A. typica* was originally collected and introduced, in the Flores Sea and off East Timor (Fig. 2). Alternatively, larvae may perhaps have entered the Banda Sea *via* the Torres Strait, although this route is less likely due to the shallowness and limited net water flow along the Strait (Wolanski *et al.* 2013). Also, the westward flow of the NGCC and the localization of the PNG specimen preclude the reciprocal scenario in which *A. typica* originated somewhere in the Philippine Sea. However, this conclusion does not contradict the possible presence of this rhodaliid near the Philippines, where it could have arrived in the Kuroshio Current. The northward flow of this current may also justify the East China Sea record of *A. typica* (Qiu 2001), which is located fairly near the northern limit of coral growth in tropical waters in this region (see Gallagher *et al.* 2015).

Although the connectivity of *Archangelopsis* species further supports our tentative identification of the PNG specimen as *A. typica*, a few doubts must remain, as no rhodaliids have yet been identified from the eastern Indian Ocean. However, given that rhodaliid life cycles most probably include what can only be a short-lived pelagic larval stage and a much longer-lived benthic stage, this attribute confers a more defined biogeographic structure upon rhodaliids than is exhibited by holoplanktonic and most meroplanktonic hydrozoan species (Gibbons *et al.* 2010). The findings of Mapstone *et al.* (2016) further support this conclusion, since geographical isolation of rhodaliids around continental shelves and on highly productive mid-ocean ridges has resulted in increased speciation in this unique benthic siphonophore family. It is likely, therefore, that the populations of *A. typica* which inhabit the Indonesian Archipelago are completely isolated from those of *A. jagoa* in the Comores Islands and the Gulf of Aqaba, both of which are probably restricted to habitats around the African continent.

Conclusions

Combining all the characters of the PNG rhodaliid discussed above, and possible tentative connectivity with *Archangelopsis typica* *via* the Indonesian Throughflow and Kuroshio Current, the image shown in Fig. 1 may represent a fourth record for *A. typica*. However, some doubt must remain, as no specimen was collected, a papillate aurophore was not discerned and tentillum placement on the tentacle segment also apparently differed. Relatively minor differences in the PNG specimen, including pneumatophore colour, nectophore circular canals and tentillum pigmentation also support the conclusion that it might be either a fourth specimen of *A. typica*, or a new species of *Archangelopsis* not yet described. It is to be hoped that this paper will alert future SCUBA divers to search for this rhodaliid in PNG waters, and also, hopefully, in other regions of Indonesia where *A. typica* has already been collected, namely just south of Kangeang Island in the Bali Sea, and also off the SE coast of East Timor in the Timor Sea.

Finally, we would like to emphasize the role of citizen science in modern-day research, and especially the possible contribution of recreational scuba divers to marine biology and ecology. The likelihood of acquiring high-resolution, underwater photographs supplemented with image metadata (*e.g.* date, geographical position, depth, type of substrate *etc.*) constitutes an invaluable, but as yet not broadly used source of scientific data, which when deposited in public databases/platforms can advance our understanding of the world's oceans.

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